HARVARD THEOLOGICAL REVIEW

VOLUME VI JULY, 1913 NUMBER 3

A BRIEF SURVEY OF THE FIELD OF ORGANIC EVOLUTION[1]

GEORGE HOWARD PARKER

HARVARD UNIVERSITY

Readers of the popular scientific magazines and papers of to-day are often confronted with the statement of the downfall of evolution; and, though this statement is usually not made in a way that carries conviction, there is a growing feeling among the educated public that behind all this smoke there is some fire. It is the object of this article to make clear the real grounds for this suspicion, and at the same time to give a brief survey of the present state of the theory of organic evolution.

One of the most profound and wide-spread movements of the last century was a growing interest in the historical aspect of nature, a movement in which the theories of the older cosmography gave place to those of modern cosmic evolution. In the midst of this movement stands the theory of organic evolution, the object of which is to explain the steps by which plants and animals have come to their present state. This theory includes the theory of descent with modification and certain explanatory hypotheses, such as Lamarck's hypothesis, Darwin's natural selection, De Vries's theory of mutations, and others. In dealing with organic evolution, I shall give, first of all, a brief account of descent with modification, and afterwards take up, for fuller consideration, the explanatory hypotheses already mentioned.

According to the theory of descent with modification, the existing species of organisms, both plants and animals, have arisen by

[1] The substance of this article was given in four lectures delivered before the Harvard Summer School of Theology, July, 1909.

the modification of pre-existing species. This theory is usually put in strong contrast with that of special creation as contained in many of the ancient sacred writings. Although descent with modification was a conception not unknown to the ancient Greeks, it is essentially a modern view. Even Linnaeus, the father of systematic botany and zoölogy, firmly believed that the number of species of plants and animals was strictly limited to those originally created. The first man of science who advocated seriously the theory of descent with modification was the French naturalist Lamarck, who lived between 1744 and 1829. His efforts, however, were without avail, chiefly because of the overpowering opposition of Cuvier; and it was not until the time of Darwin, nearly half a century later, that descent with modification was accorded a fair hearing. After the publication of *The Origin of Species* in 1859, the theory of descent steadily gained ground till at present practically every biologist of any standing whatsoever accepts it. This change on the part of naturalists from an attitude of hostility toward this theory to one of general acceptance was brought about by the accumulation of evidence from at least four independent lines of research: palaeontology, zoögeography, embryology, and comparative anatomy.

The work of the palaeontologist has shown that notwithstanding the enormous obliteration of organic remains in the past, enough have been preserved in the form of fossils to give some idea of the ancient faunas and floras of the earth. When these are compared with one another, it is quite evident that the more ancient the deposit the less do its organic contents resemble the animals and plants of today, and yet between any ancient deposit and that of the present the organisms exhibit a continuity such as would be presupposed by the theory of descent with modification. In many species, as for instance the modern horse, the genealogy of the animal has been worked out with wonderful completeness and detail.

Zoögeography, the study of the distribution of animals, has also contributed much to the advancement of the theory of descent. As a result of such studies it has been shown that the existing animals of a given region are more nearly related to the fossils of that region than they are to the fossils of other parts of

the earth's crust. This is strikingly illustrated by the sloths and armadillos. The modern representatives of these animals are limited to the American continent south of the United States. The fossil sloths and armadillos, though very unlike the modern species, are restricted to approximately the same area of the globe. Such facts in zoögeography are easily understood from the standpoint of descent with modification, but are not particularly significant from that of special creation.

One of the chief generalizations of embryology is to the effect that in the course of the development of the higher animals, they pass through stages that resemble permanent conditions in the lower forms. Thus it has long been known that the embryos of reptiles, birds, and mammals, the air-inhabiting vertebrates, exhibit in the region of the neck gill-clefts which disappear before birth but which correspond to those permanently present in the water-inhabiting forms, the fishes. Many other like examples might be cited. Why the embryos of higher animals should resemble in certain particulars the permanent conditions of the lower animals is not clear from the standpoint of special creation; but from that of descent with modification these conditions in the higher animals are easily interpreted as repetitions of the steps in their evolution. So much of the development of individual animals is made up of a succession of features of this kind that it is now generally believed that each animal in its growth from the egg to maturity passes through a series of stages that portrays, at least dimly, the evolution of its race, or, to put it as Huxley has facetiously done, each animal in the course of its development climbs its own ancestral tree. This state of affairs has been expressed in the generalization known as the Law of Recapitulation, a generalization entirely in accord with descent with modification but quite meaningless from the point of view of special creation.

Finally, from the standpoint of comparative anatomy a fundamental similarity has been discovered in organs correspondingly situated in different animals. Thus it has been shown that the front leg of a quadruped, the wing of a bird, and the arm of a man all possess an internal structure strikingly similar, and are all based upon the plan of structure seen in the pectoral fin of the

fish. These facts have no particular significance from the point of view of special creation, but they are full of meaning when regarded in the light of descent, for they are indicative of blood-relationship.

Furthermore many animals possess organs that are useless and rudimentary, though in other closely related species the corresponding parts may be of the utmost functional value. Thus man possesses muscles for moving the external ear, a vermiform appendix, and other parts, none of which is of any apparent importance to him, though these very parts in the lower mammals are highly developed and functional. Wiedersheim enumerates over a hundred such organs in man alone. What rudimentary organs signify from the point of view of special creation has never been clearly shown. From that of descent with modification they are obviously organs in process of disappearance, and as such lend support to this theory.

The accumulated evidence from the four lines of research, palaeontology, zoögeography, embryology, and comparative anatomy, has gradually grown to such a volume and is in such close accord with the theory of descent that biologists have completely abandoned any other explanation for the present state of the plant and animal kingdoms. Descent with modification is so universally accepted at present that one seldom hears it even mentioned. It may be regarded as one of the established facts of biological science. Whatever there is of uncertainty and dispute concerns not descent with modification, but the way in which descent is supposed to have been accomplished. On this point there is room for much difference of opinion. Of the chief questions in Darwin's day, descent with modification and the methods of accomplishing this, the first, for reasons already given, has been definitely answered in the affirmative; the second is still unsettled. It is my intention in the remainder of this article to take up the three most important explanations that have been brought forward for descent with modification, namely, Lamarck's hypothesis, Darwin's natural selection, and De Vries's theory of mutations.

The substance of the Lamarckian hypothesis is perhaps best stated in Lamarck's *Philosophie zoologique* published in 1809.

In this work the author emphasizes the great importance of the influence of the environment, and he distinguishes what may be termed a direct and an indirect method of influence. Of these the first is well exemplified in many plants. Lamarck, who was a trained botanist as well as a zoölogist, observed that the white water-crowfoot, a common European plant, had finely divided leaves where it grew under water and longer and more simply lobed leaves where it grew in the air. Thus the same plant took on quite different aspects, depending upon its immediate surroundings. The environment then, according to Lamarck, affects *directly* the form of the organism, and hence a changing environment may be a potent factor in bringing about descent with modification. But the environment also exerts a very important *indirect* effect on organisms, an effect which is best seen in animals. To meet a change in the environment, an animal may change its habits, and in changing its habits it may exercise its body so as to increase the development of certain parts or decrease that of others. These bodily changes, the product of use and disuse, when inherited from generation to generation, may so change the individuals that the transformation of one species into another may be accomplished; in other words, descent with modification may take place. Lamarck illustrated this form of environmental influence by his well-known example of the giraffe. He believed the peculiar form of this animal to have been produced by the conditions in central Africa, where the earth is nearly always dry and without herbage and the animals, according to Lamarck at least, are in consequence obliged to browse on the foliage of trees. As a result of this practice, the front legs and especially the neck of the giraffe have been exercised and lengthened generation after generation till the modern form of the animal has been assumed. Thus the ancestor of the giraffe through a change of habit induced by the environment was metamorphosed into the present animal, an *indirect* product of the environment. These in brief are Lamarck's views of the way in which the environment directly or indirectly moulds the organism and thus brings about descent with modification.

Two serious objections can be brought against Lamarck's principles: first, they apply to only a limited range of the features

and activities of organisms, and, secondly, they necessitate a belief in the inheritance of acquired characters. Although Lamarck's principles seem to hold for structures such as bones, muscles, and the like, in the development of which use and disuse may obviously play an important part, it is difficult to understand how these principles can be made to apply to other aspects of organisms, such as protective coloration. Many animals have a most striking resemblance to certain features in their environment; thus moths resemble in coloration the bark of the trees on which they habitually rest, the walking-stick insects are scarcely distinguishable from the twigs amongst which they live, the northern hare has a dun-colored coat in summer and a white one in winter in conformity with the covering of the earth at these seasons. These conditions and a host of others can scarcely be supposed to depend upon the direct or indirect effect of the environment; use and disuse can have had no part in bringing them about. The Lamarckian principles do not seem to afford any very satisfactory explanation of the origin of these phenomena. Many Lamarckians meet this situation by belittling or even denying the existence of protective coloration, but though this attitude may be correct as regards certain extreme examples of so-called protective coloration, it certainly does not hold for the majority of such cases. It therefore follows that even if we admit that the Lamarckian hypothesis is a real factor in explaining descent, it can be successfully applied to only a limited range of the phenomena which any complete explanation of descent must take into account.

Lamarckism, however, is not only thus limited in its application, but even where it seems to apply, it must meet the very serious difficulty of the inheritance of acquired characters. The ground for this criticism, which is one of the cardinal points with the neo-darwinists, is Weismann's chief contribution to evolutionary theory. Weismann very clearly pointed out that in animals that reproduce sexually the body is composed of two fundamentally distinct classes of cells: the reproductive or germ cells (the egg cells in females and the sperm cells in males) and the body cells or somatic cells, such as the cells of skin, bone, or muscle, which make up the great bulk of the body of any indi-

vidual. Weismann further pointed out that since acquired characters are those characters which an organism gains in the course of its individual life by the direct or indirect effect of the environment, by the use or disuse of its parts, they are of necessity changes in its somatic cells, such as the muscle-cells or skin-cells, and since these cells have no observable means of impressing their changed states on the reproductive cells, and die with the death of the individual, there is good reason to believe that acquired characters are never inherited. If this is so, Lamarckism, as Weismann argues, is an impossible explanation of descent with modification.

To ascertain whether the somatic cells have such an influence on the germ cells as to reproduce in the offspring conditions acquired by the parent, Weismann undertook a long series of experiments on the heritability of mutilations. Most mutilations are, of course, changes in the somatic cells, and the question that Weismann had in mind was whether these changes would so affect the germ cells of the individual on which they were wrought as to reappear in its offspring. To test this question the following experiments were tried. The length of the tail was measured in a certain number of mature mice, and these animals were then mutilated by cutting off their tails. They were then bred among themselves, and the lengths of the tails of their descendants were measured after these descendants had become mature. The tails of the first generation of descendants were then cut off and from these animals a new generation was bred, and so on. After nineteen such generations had thus been produced and mutilated, the average length of the tails of the last generation was found to be still the same as that of the first. These experiments have been confirmed on rats and mice by numerous other investigators; and it is now generally admitted that acquired characters, such as mutilations, are not inherited. This conclusion is supported by what is known of many practices of the human race, such, for instance, as circumcision, which has apparently had no influence on the size of the foreskin of the Hebrews.

Although the outcome of the experiments and discussion called forth by Weismann's declaration that such acquired characters as mutilations are not heritable has led most biologists to accept

this conclusion, it is far from proved that acquired characters of another kind, such as those that depend upon the normal action of parts, may not be transmitted. Conclusive experiments of this kind are, however, extremely difficult to devise and carry through. One of the most satisfactory lines of work in this direction is that which is based upon transplanting germ cells. If the somatic cells can impress their characteristics on the germ cells, then germ cells taken from an individual having one set of somatic characters and allowed to develop in another individual with a different set of somatic characters ought in time to show the effects of the new somatic environment. Experiments based upon this line of investigation have been carried out recently by Castle and Phillips on guinea pigs.

The question tested by these investigators was the influence of color of the hair of the guinea pig on the germ cells contained within its body. That the nature of the experiment may be fully appreciated, it is necessary to state in advance that when a pure race of albino guinea pigs is crossed with a pure race of black guinea pigs, the offspring in the first generation are always all black. Bearing this in mind, the following experiment was performed. A female albino guinea pig just attaining sexual maturity was by an operation deprived of her ovaries and in place of the removed ovaries there were introduced into her body the ovaries of a young black guinea pig. Thus the germ cells of a black stock were placed under the influence of a white body. Will the white-haired body of the foster-mother influence the introduced germ cells of the black stock? To test this the foster-mother was mated with a pure albino male. She bore three litters of young, the first about six months after the operation, the last about a year after it. These three litters consisted in all of six individuals and all were as black as the female from which the ovaries had been obtained. Thus it is clear that, so far as the color of the hair is concerned, the somatic conditions of the white stock had no influence in the course of a year on the germ cells of the black stock. Experiments and observations of this kind are not numerous, but, so far as they go, they support the contention that somatic changes in the nature of acquired characters do not influence the germ cells so as to reappear as such in the offspring;

in other words, they support Weismann's contention that acquired characters are not inherited.

Viewed from the standpoint of daily experience, this conclusion seems contrary to all we know. Most persons believe that the industrious or slothful habits of the parent have their influence on the child, but, as a matter of fact, the question in man is a much more complex one than in most other animals. Man is a social being with powers of imitation, and much that we say we have inherited from our parents has come to us in this way. Human inheritance in a broad sense may be said to be made up of physical inheritance, such as that illustrated by the color of the hair, and of what may be called social inheritance, which is dependent upon imitation and is, therefore, mostly educational. In the case of a given trait in an adult man or woman, it is not always easy to say whether it has been inherited physically, that is, is congenital, or whether it has been inherited socially, that is, has been learned. The socially inherited traits, our educational activities from childhood onward, have no bearing on the question of the inheritance of acquired characters as this term is used by the biologist, but they do afford the material which in the popular mind often leads to an acceptance of this view. Yet if the distinction in man or other colonial animals of the two forms of inheritance, physical and social, is kept in mind, confusion will be obviated and man, like other animals, will be found to have afforded thus far no conclusive evidence for the inheritance of acquired characters. The principle of the inheritance of acquired characters is apparently essential for the Lamarckian hypothesis and, since it has thus far failed to receive the support of observation and experiment, the most that can be said for Lamarckism is that, though it may be a possible factor in organic evolution, it is a very improbable one.

The second important explanation offered for descent with modification is Darwin's theory of natural selection, or, as it is often simply called, Darwinism. This theory, which was simultaneously advanced by Charles Darwin and Alfred Russel Wallace, is most fully and exhaustively presented in Darwin's *Origin of Species,* published in 1859. From early manhood Darwin had been interested in the problem of the origin of species, and this

interest led him to look into the origin of domesticated stocks such as the various kinds of dogs and pigeons. On examining the methods employed by animal-breeders, he found that to obtain a stock with a given trait the breeder selected for breeding purposes those individuals that showed some evidence of the desired trait and, continuing this process with the offspring generation after generation, eventually obtained a stock with the desired character in full development. This operation of selection Darwin called artificial selection. He believed that an analogous process could be shown to occur in nature; and this process, which he called natural selection, was in his opinion a sufficient explanation for the origin of species.

The grounds given by Darwin for his belief that natural selection actually took place, may be stated briefly in the following way. Darwin saw clearly that even in plants and animals that reproduced most slowly there were more descendants formed than could possibly reach maturity. He estimated in the case of the elephant, probably the slowest-breeding animal known, that the descendants of a single pair, supposing all the young to live to maturity, would after about 750 years amount to almost nineteen million. That elephants are not increasing at this rate is obvious; hence it is fair to assume that all organisms are producing more offspring than can possibly reach maturity.

The second fact that Darwin recognized was that all individuals, plants as well as animals, differ from one another. As every one knows, even animals of the same litter differ in color, strength, disposition, to such a degree that they are easily and quickly distinguishable. This variability occurs in nature as well as under domestication, and is one of the most conspicuous as well as the most fundamental properties of organisms.

If, now, more offspring are produced than can possibly survive and every individual in the race differs from the others, it follows, as Darwin argued, that those individuals that show slight advantages over the others will in the long run tend to survive, and thus, through a process of natural selection, the individuals possessing advantageous variations will be preserved and allowed to breed and those with disadvantageous features will be eliminated. This process, often spoken of as the struggle for existence, or the sur-

vival of the fittest, would tend to adapt organisms more and more closely to their surroundings, and if the environment was in slow but continuous change, descent with modification would result.

It will be seen at a glance that Darwin's method of explaining descent is based upon fundamentally different principles from those used by Lamarck. The contrast between natural selection and Lamarckism can perhaps be more fully appreciated if we attempt to portray, from the standpoint of the two theories, the steps by which the giraffe's neck may be supposed to have originated. According to Lamarck, as already pointed out, the giraffe's neck was believed to have been lengthened by adding together from generation to generation the slight increments due to the exercise of each individual in reaching upward into the foliage. According to Darwin this lengthening may be considered as due to the elimination in periods of stress of the individuals with shorter necks and the preservation till the breeding period of those with longer necks. Thus Darwinism supposes that lasting modification is occasioned by inborn differences rather than by acquired characters, and it must be evident that it covers all the cases that Lamarckism does. But Darwinism not only covers the same ground that Lamarckism does—it covers more. It explains with complete success such cases as protective coloration, which were by no means easy to understand from the point of view of Lamarckism. Animals whose coloration blends less successfully with their environment are more likely to fall a prey to their foes than those whose markings imitate more truly the backgrounds on which they rest. Thus natural selection can be as effective in cases of protective coloration as in those which have to do, for instance, with muscular activity.

Furthermore, Darwinism does not necessitate a belief in the inheritance of acquired characters. Selection is supposed to be accomplished on the basis of inborn traits which appear in the course of the development of the individual and which, being congenital, are consequently handed on in the germ cells from generation to generation. In this respect natural selection is free from the most serious obstacle that Lamarckism has to contend with.

Weismann, as the central figure among the neo-darwinists, in denying the inheritance of acquired characters, has declared that

natural selection of itself is a complete and sufficient explanation of organic evolution, while others, the neo-lamarckians, have in many instances been inclined to take the opposite view. But though there are well-marked contrasts, as just pointed out, between Lamarckism and Darwinism, it must not be supposed, as many investigators seem to have done, that there is any fundamental antagonism between the two theories. Both may be effective at once. The real question is whether either of them is a true factor in organic evolution. An interesting and significant combination of the two theories has come from several recent investigators, namely, Osborn, Baldwin, and Lloyd Morgan. This combination has been called by some "organic selection" and rests on the idea that a trait which has appeared as an acquired character, and which is retained generation after generation by the continuous action of the environment, may help to preserve a certain stock of individuals till natural selection can reproduce and establish this trait as a germinal character. Thus organic selection is to a certain degree a combination of the principles of both Lamarckism and Darwinism.

But Darwinism, like Lamarckism, is not without its serious objections. For almost half a century it has served as a convenient and acceptable theory for biologists to use in explaining the origin of useful traits in organisms, but in the last decade, during which evolution has changed from a speculative to an experimental science, objections to it have become stronger and stronger, till not a few botanists and zoölogists have come to regard it, not merely as an inadequate and partial explanation, but as absolutely ineffective. It is this charge of ineffectiveness made by a few of the more radical biologists that has unsettled the public mind about evolution in general. But from what has already been pointed out, it must be clear to the reader that this charge affects only Darwinism, one of the explanations of descent with modification, and has nothing whatever to do with descent itself. Those who oppose Darwinism most strenuously are as a rule vigorous supporters of the theory of descent; their contention is that Darwin's particular explanation of descent is probably incorrect.

The chief objection that has been raised against natural selec-

tion is one which was well known to Darwin himself, but which has been gathering strength for some years past. It is to the effect that the initial phases of a favorable variation, as conceived by Darwin, are too slight to be of use to the organism, and consequently they cannot come under the influence of the selective process. When the slight individual differences that Darwin laid so much stress upon are closely scrutinized, it seems scarcely conceivable that they could be, even in the long run, of life-and-death importance to an organism; in other words, that they could afford a starting-point for the formation of a new species. And when closely related species in nature are examined, such as the different kinds of warblers, or of sedges, it seems impossible that the slight differences separating them should represent gaps produced by natural selection through an elimination of intermediate forms. Thus an inspection of nature reveals a state of affairs which many investigators have come to believe to be much too refined to be a product of natural selection.

Attempts to show that natural selection is taking place have been more or less successful, and their results are extremely instructive. Bumpus has reported the selective effect of a severe winter ice-storm on sparrows. After a storm in Providence, R.I., on February 1, 1898, many of the sparrows of that region were found to be much spent and exhausted. Of these birds, 136 were collected and brought within doors, and of this number 72 revived and 64 died. Do these two groups represent two classes of animals, one with slight advantageous the other with slight disadvantageous traits? Careful measurements of spread of wing, weight of body, etc., revealed the fact that the birds that died were less near the normal than those that survived, showing that a heavy body with small wings, or a light body with large wings, etc., was disadvantageous under stress of circumstances as compared with a body of average weight carrying wings of average extent. In this instance, then, natural selection was certainly effective, but it eliminated only the most unfit and was not concerned, so far as could be seen, with those slight differences that make up the distinguishing traits of species. Observations of this kind, as well as the general impression made by inspecting closely related species in nature, has led to the conclusion that

natural selection, though a real factor in explaining descent with modification, is only a partial one. To state the matter in a figurative way, natural selection may be said to be capable of rough-hewing a species but not of putting on the polishing touches. If this conclusion is admitted as substantially correct, it is evident that Darwinism, unlike Lamarckism, must be admitted to be an effective factor in bringing about descent with modification, though its rôle in descent is apparently much less significant than was formerly supposed to be the case.

The objection to natural selection discussed in the preceding paragraphs is not the only one that has been raised. It is, however, the chief one. Students of this subject have called attention to the fact that many organs in animals and plants seem to be more highly specialized than is needful, a valid objection to natural selection as an all-sufficient process. It has also been pointed out that even if we grant that through natural selection advantageous characters were to get a foothold, yet in the beginning individuals possessing these characters would be obliged to pair with others that did not possess them, and thus the new traits would tend to be swamped out and so obliterated. To meet this objection subsidiary hypotheses having to do with isolation, either geographical or physiological, have been devised and put forward, but many of these minor objections have now been minimized, if not entirely swept away, by the recent advances in our knowledge of the laws of inheritance. These have afforded the basis of the modern experimental treatment of evolution, and centre particularly around the names of Mendel and De Vries, the latter of whom is the author of the mutation theory.

The mutation theory, together with what it implies, is undoubtedly the most important single contribution to the theory of organic evolution since the promulgation of the theory of natural selection. Historically it is the third of the major attempts at explaining descent with modification. It is well set forth by its author, Hugo De Vries, in his work entitled *Die Mutationstheorie*, the first part of which appeared in 1901.

According to De Vries the characteristics of organisms are made up of elementary units which are as sharply separated from one

another as the chemical elements. These unit-characters show no intergrades, and any combination of them constitutes what De Vries calls an elementary species. Although these general statements were based by De Vries on a study of plants, particularly on the evening primroses, they have been found to be equally applicable to animals. Thus the color and other conditions of the hair of guinea pigs afford excellent examples of unit-characters. Some guinea pigs are entirely white, others entirely black, and still others are piebald; again some have short hair, others long hair; some have smooth hair, others rough. All these characters are unit-characters and any combination of them may be made, and constitutes, according to the views of De Vries, an elementary species. Thus a guinea pig with smooth, short, black hair belongs to a different elementary species from one with rough, short, black hair, and these two species differ in only one unit-character.

Guinea pigs are known that have rough, long, white hair, thus differing from the first elementary species just mentioned in all three unit-characters. In fact each new combination is a new elementary species. To the older systematists the guinea pig was supposed to be a single species, but from this point of view it is an aggregate of elementary species. De Vries, therefore, calls the species of the older naturalists collective, or Linnaean, species, and this newly described kind, elementary species. Elementary species, then, are separated from one another by the possession of different unit-characters and hence by a cleft unbridged by any intergrades.

De Vries investigated with great care the origin of elementary species and the principles on which unit-characters are inherited. In the course of this work he rediscovered much that had already been brought to light by Mendel nearly fifty years before, but had escaped the attention of biologists. These generalizations, now usually known as the Mendelian principles, are thus the independent discoveries of Mendel and De Vries, and have been abundantly confirmed on both animals and plants. They may be illustrated by the results obtained from breeding guinea pigs, and they are most clearly followed when individuals differing in only one unit-character are used. If a guinea pig of pure breed

whose coat-color is black, is mated with a pure white one, all the offspring, constituting what is known as the first filial generation, are black. If these guinea pigs are now bred among themselves, they will produce a population composed of definite proportions of white and of black individuals. Twenty-five per cent of this population will be composed of pure white individuals and seventy-five per cent of black ones, of which one-third will be found on being tested to be pure black and the other two-thirds to be black, but capable, like their parents, of producing white individuals. Thus the second filial generation is composed of one-quarter pure whites, one-quarter pure blacks, and one-half blacks which, however, will produce some whites. As Mendel pointed out, this second filial generation contains in these remarkable proportions individuals that represent perfectly the parents and grandparents of the stock; for the pure white individuals and the pure black ones are like the grandparents both in appearance and in breeding capacity, while the fifty per cent blacks that will produce some whites are exactly like the black parents in the first filial generation. One of the most remarkable features in simple Mendelian inheritance is that the larger the number of plants or of animals bred, the nearer do the numbers of the several classes in the second filial generation approximate the proportions given, so that there is good reason to believe that these proportions represent real relations.

Mendel was so impressed by the invariableness and definiteness of these hereditary relations that he was led to formulate an explanation the assumptions of which seem even at present to be admitted by most workers in this field. He pointed out that, since the second filial generation was composed of individuals some of which had the character of one grandparent, others the character of the other (in the case of the guinea pig a white coat or a black coat), therefore the first filial generation, although apparently entirely of one character (black in the guinea pig), must carry the other character hidden in it. Hence he declared that in the case of a pair of characters, such as white and black coat-colors in guinea pigs, one might dominate over the other, and that character which thus gained the ascendency he called *dominant*, the hidden one *recessive*. In guinea pigs it is well established

that black—or in fact any color, including the piebald state—is always dominant over white, which is, therefore, recessive. It is also known that short hair is dominant over long hair, and rough over smooth hair.

The second assumption that Mendel made was to the effect that the germ cells, both egg cells and sperm cells, were pure in respect to the unit-character they carried, and this he believed gave an explanation of the very remarkable proportions met with in the several classes of the second filial generation. He assumed that each egg cell or sperm cell could carry only one of the two opposing unit-characters, and that in this respect it could be said to be pure. With this assumption in mind we may now consider the course of events in the three generations of guinea pigs already described. In the two individuals with which the experiment is assumed to start it makes no difference whether the male or the female is white, the outcome will be the same in either case. If we assume that the male is of pure white stock then, on the basis of Mendel's belief as to the purity of the germ cells, we should expect that all the sperm cells produced by this individual would carry the character white and no other. If the female is of pure black stock, then all her egg cells would in like manner bear the character black. Since every organism that has been produced by ordinary sexual methods arises from an egg cell fertilized by a sperm cell, it follows that each offspring resulting from the mating of this pair of animals would come from an egg cell with the black character combined with a sperm with the white character. This combination would in all cases give individuals in which both traits were present, but in which, of course, the black would be dominant over the white, so that all the members of the first filial generation would be black. If now we continue to assume the purity of the germ cells, the males of this generation, since they contain both characters, ought to produce two kinds of sperm cells, those with the character white and those with the character black. Similarly, the females ought to produce two classes of eggs, which we may call, for the sake of brevity, white eggs and black eggs. If, now, we imagine that the two classes of eggs and the two classes of sperms are produced in equal numbers and that their combinations in fertiliza-

tion are purely fortuitous, an interesting proportional relation is arrived at for the second filial generation. It is obvious that there are four possible combinations among the two classes of sperm cells and of egg cells. Once in four a white egg will be fertilized by a white sperm, and this combination will give rise to the twenty-five per cent pure white individuals in this generation. Once in four a black egg will be fertilized by a black sperm, and this will produce the twenty-five per cent pure black stock. Once in four a white egg will be fertilized by a black sperm and also once in four a black egg will be fertilized by a white sperm, and these two classes will produce together the fifty per cent. of black individuals, which, however, are capable of bearing white young. Thus the assumption of the purity of the germ led Mendel to an explanation of these remarkable proportions so frequently observed in the second filial generation. Because of this correspondence and many others based upon other combinations, the purity of the germ, or, as it is often called, the segregation of characters, is believed to be of fundamental importance in breeding; and this conception together with that of dominance, already alluded to, constitutes the chief features in what are often called the Mendelian principles.

These principles, as must be evident, are in complete harmony with De Vries's idea of elementary species, for they show how unit-characters act in heredity, how they are handed on from generation to generation unimpaired and unconfused. They afford in this way a firm basis for De Vries's mutation theory. De Vries maintains that when the differences between individual animals or plants are closely scrutinized, they are found to fall into two distinct categories: the small fluctuating differences that Darwin laid so much stress on in his theory of natural selection, and the larger unit-character differences such as we have seen to exist between the so-called elementary species. The small differences De Vries calls variations; the larger differences, which Darwin considered under the head of sports, De Vries calls mutations. De Vries believes, contrary to the opinion of Darwin, that variations, as just defined, have nothing whatever to do with organic evolution, but that evolution is effected by mutations, by sudden considerable jumps. This in brief is the essence of

his theory. Organic evolution, then, is accomplished by occasional strides rather than by many oft-repeated short steps. This theory is in no sense antagonistic to natural selection. In fact, it works effectively only in conjunction with natural selection, for, after all, what determines whether a race showing a trait produced as a mutation will survive or not is natural selection. The great advantage that the mutation theory has over natural selection, as stated in the old way, is that it obviates at once the difficulty of explaining how a new trait which in its incipiency was too slight to be really useful to an organism could be brought forward to a useful condition by natural selection. Mutations do not arise by any such gradual process but spring fully formed into existence and therefore are at once in a condition to be acted upon by natural selection. The mutation theory, then, affords a most successful means of overcoming the chief obstacle to natural selection, but, as De Vries himself rightly maintains, the mutation theory is significant only in connection with natural selection.

The Mendelian principles and the mutation theory both imply in the process of inheritance a certain rigidity, a certain inelasticity, not ordinarily associated with organic nature. Under these conditions the guinea pig may have either a white coat or a black coat; it cannot have all the intermediate grays, as is implied, for instance, in Galton's theory of ancestral inheritance. And it must be confessed that there is some justification for this idea of rigidity. Evidence of this kind of reproductive inelasticity is not easily obtained from organisms that reproduce by cross-fertilization (a male individual fertilizing the eggs of a female individual) as most animals do, but is more clearly seen when self-fertilization is accomplished, as in many plants, or where the organisms reproduce without fertilization, as among the protozoans, the simplest animals. Investigation in this direction has given rise to what are known as pure-line cultures, first worked out among plants by the Danish botanist Johannsen and among animals by Jennings, who has studied inheritance in the slipper-animalcule, or paramoecium. This animalcule, which is shaped somewhat like a slipper and is just visible to the naked eye, grows in great numbers in stagnant water. If a large popula-

tion is examined, it will be found to be made up of individuals that vary considerably in size, the largest being perhaps seven to eight times the size of the smallest. These animalcules ordinarily reproduce by the simple process of dividing in two and then growing in size. If, now, one of the largest individuals is taken and its descendants observed through many generations, it will be found not to be able to reproduce the condition of the whole population, for its descendants will always be more or less large. In a similar way small individuals will give rise to a stock whose members never attain to the size of the larger members of the whole population. Thus it is clear that in a population of animals—and the same is true of plants—where reproduction is not accomplished by the continual crossing of individuals, the population is composed of separate lines kept within certain bounds,—a condition which supports the general conception of the relative inflexibility of the hereditary process.

But notwithstanding the fact that many characters are inherited in a strikingly rigid way, others are apparently inherited quite differently. Thus when the black race and the white race cross, the offspring is neither a black nor a white individual, but a person of intermediate tint, a mulatto. This form of inheritance, which is often called blended inheritance, is also illustrated by certain characteristics in the lower mammals. If a long-eared rabbit is crossed with a short-eared one, the offspring have ears of intermediate length, and if the rabbits with ears of intermediate lengths are crossed with the long-eared or the short-eared stocks, new intermediate stocks are produced with lengths of ears midway between those of their parents. Thus blended inheritance presents conditions apparently wholly unlike those met with in the ordinary Mendelian scheme. It is true that some investigators have maintained with a good deal of reason that blended inheritance after all is only a disguised form of Mendelian inheritance in which dominance is absent; but, however this may be, blended inheritance shows very clearly that under certain circumstances the rigidity of inheritance is not so marked as it appears to be in the true Mendelian cases.

But more or less direct evidence for the modification of the so-called unit-characters has from time to time also been forthcom-

ing. Castle and Phillips have described a case of this kind in hooded rats. These animals have a whitish coat except for a black, hood-like splotch on the head and a similar streak down the middle of the back. This character behaves as a Mendelian recessive when crossed with the ordinary gray of the common rat. By long-continued selection, as prescribed by Darwin, there were obtained from the ordinary hooded rats two extreme conditions, one in which the hood and stripe were so reduced that the animal was almost an albino, and the other in which these areas were so expanded as to give the animal almost the appearance of a gray rat with a white belly. These two extreme stocks, nevertheless, bred true, and on being crossed with the common gray rat the extreme conditions reappeared in appropriate Mendelian proportions. It appears, therefore, that though many characters are inherited in Mendelian fashion, all are not necessarily so inherited; and even Mendelian characters are open to modification by selection. This is perhaps the most significant criticism that can be made against the mutation theory, the introduction of which has revolutionized the field of organic evolution from that of an observational science to an experimental one. Till this new method of attack has yielded further results, it is perhaps premature even to attempt to pass judgment on the mutation theory.

In conclusion, the substance of the preceding pages may be summarized as follows. The theory of descent with modification is an established fact. As an explanation of descent, Lamarckism is a possible but unlikely factor because of the improbability that the inheritance of acquired characters takes place. Darwinism, or natural selection, on the other hand, is apparently a real factor in organic evolution, at least roughly outlining natural species. Its chief defect, the inability to produce useful traits from small beginnings, is apparently fully met by the mutation theory, which, however, is too novel to be passed on with any degree of certainty. The popular distrust which has recently arisen concerning evolution is based on a confusion of natural selection with descent. As to the effectiveness of the former the biologist has good reason for doubt, as to the reality of the latter he has none whatever.

REFERENCES

Bateson, William.
Mendel's Principles of Heredity. Cambridge, University Press, 1909.
A discussion of the modern aspect of Mendel's principles together with a biographical account of Mendel and translations of his principal papers on heredity.

Castle, William E.
Heredity in Relation to Evolution and Animal Breeding. New York and London, D. Appleton and Co., 1911.
A clear and readable account of modern theories of heredity.

Darwin, Charles.
The Origin of Species by Means of Natural Selection. With Additions and Corrections from Sixth and Last English Edition. New York, D. Appleton and Co., 1895.
The authoritative statement of Darwin's theory of natural selection.

Delage, Yves, and Goldsmith, M.
The Theories of Evolution. Translated by A. Tridon. New York, B. W. Huebsch, 1913.
A general account of the theory of evolution with emphasis on Lamarckism.

De Vries, Hugo.
Species and Varieties; their Origin by Mutation. Chicago, Open Court Publishing Co., 1905.
An authoritative statement of the mutation theory.

de Lamarck, Jean B. P. A. M.
Philosophie Zoologique. Paris, 1873.
The authoritative statement of Lamarckism.

Morgan, T. H.
Evolution and Adaptation. New York, The Macmillan Co., 1903.
An excellent general account of the modern theory of evolution.

Osborn, H. F.
From the Greeks to Darwin. New York, The Macmillan Co., 1894.
An excellent history of the theory of descent.

Weismann, A.
The Evolution Theory. Translated by J. A. Thomson and M. R. Thomson. London, Edward Arnold, 1904.
Neo-Darwinism stated by its chief advocate.